Modeling Population And Ecosystem Response To Sublethal Toxicant Exposure

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LONG TERM GOALS

The ecological effects of environmental stress occur within complex communities and ecosystems. The PIs have recently developed and tested general dynamic energy budget models characterizing the response of individual organisms to toxicants, and developed methodology for using these models to predict population dynamics. They have also developed new theory describing the trophic dynamics of open systems. They now propose to use these advances as the basis of research to test the predictive power and limitations of an individual-based approach to understanding the impact of pollutants on the dynamics of marine communities and ecosystems with multiple trophic levels.

OBJECTIVES

The research has three main components:

a) Models of the acclimation of individual organisms to changes in their environment.
b) Development of simple models of marine organisms in open populations competing for a single resource in a polluted environment. Tests against data on estuarine fish experiencing environmental gradients.
c) Development of simple ecosystem models with primary producers, competing herbivores and explicit incorporation of microbial dynamics. Tests of the models using experimental data on polluted benthic microcosms obtained by Dr. Kevin Carman (Louisiana State University). Use of the models to interpret field data on infauna near point sources of pollution.

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APPROACH

We use different but related models for our different objectives. Underpinning all the research are *dynamic energy budget* (DEB) models of individuals. We use simple DEB-based *individual-based models* to describe changes in structure and biomass of populations. We are developing ecosystem models that describe the flow of elemental matter in a way that is consistent with the DEB models of individuals.

Dynamic energy budget models

Toxic compounds may reduce the fecundity, development rate, and/or survival probability of *individual organisms*. These changes can be modeled using dynamic energy budget (DEB) models incorporating information on the physiology of individuals (Kooijman 1993; Nisbet et al. 1999). DEB models use differential equations to describe the rates at which individual organisms assimilate and utilize energy from food for maintenance, growth, reproduction and development. These rates depend on the state of the organism (age, size, sex, nutritional status, etc.) and the state of its environment, (food density, temperature, toxicant levels, etc.). Solutions of the model equations represent the life history of individual organisms in a potentially variable environment.

Individual-based models of populations

Individual based models (IBMs) treat a population as a collection of individuals, each growing, reproducing and dying in response to its physiological state and to the local environment. We use IBMs in which the physiology of individuals is described by a DEB model. Previous research on zooplankton dynamics (Nisbet et al. 1997), and related research on microbial populations (Kooijman 1993) has established that in a wide range of situations, we can successfully predict biomass changes using simple ordinary differential equations, derived by making special assumptions that simplify our DEB models. Where possible, such simplified descriptions are used in the current work.

Community dynamics

The cornerstone of traditional ecological theory of competition is the competitive exclusion principle, which asserts that two or more species cannot coexist on a single resource. However, the scope of much of this theory is restricted by the assumption of “closed” populations, where recruits are the offspring of existing members of the population and the effects of immigration and emigration are negligible. We recently developed competition theory for “open” benthic systems with individuals recruited from the open ocean at rates determined by external factors and not by local population size (Wilson et al. 1998). This theory exploits the biomass-based approach described above, our criterion for two species to “coexist” being that each can grow in the presence of the other.

Modeling ecosystems

In ecosystems, the state variables no longer relate to populations, but to functional groups of populations (e.g. decomposers, primary producers and herbivores) or to the chemical make-up of the constituent populations and the environment. The full potential of DEB models for marine ecosystem modeling remains an open issue, but existing models of the flow of energy and elements (e.g. Ross et al., 1993a; Gurney and Nisbet, 1998; chapter 7) make a convincing case that ecosystems do truly have dynamics that can be described by relatively simple, general, models. Our research exploits one important property of DEB-based ecosystem models: the capability to link the description of biological and chemical phenomena. The development of appropriate methodology is part of the on-going research; as a starting point we use a model developed by Kooijman and Nisbet (1999) of mass and energy turnover in a closed ecosystem with primary producers, herbivores and decomposers. Individuals at each trophic level grow and reproduce in accordance with a DEB model. Assumptions

on stoichiometry enable calculation of the fate of up to 16 compounds. Important quantities predicted include carbon dioxide production, oxygen consumption and ammonia production.

WORK COMPLETED

Highlights of FY99 include:

- Completion of a study of dynamics predicted by a DEB model for organisms experiencing a variable environment. This is the first stage of a study of models describing acclimation of organisms to environmental stress.
- Generalization of an approach to modeling competing benthic herbivores.
- Formulation and testing of a model of competition between two species of estuarine fish.
- Study of a simple model of experiments by Dr. Kevin Carman on polluted benthic microcosms.
- Development of ecosystem models with simultaneous energy flow and recycling of elemental matter.

RESULTS

Modeling growth and reproduction in variable environments

We studied the production and survival of organisms in variable food environments using the κ-rule model developed by Kooijman (1986). Our investigation yields the following predictions. Organisms grow bigger in a variable food environment than in a constant environment with similar average food availability. Ultimate size increases with the amplitude and period of deterministic food cycles, and with the intensity and coherence time of stochastic food fluctuations. In variable food environments, organisms grow to a size related to the peaks in food availability rather than the mean. Food fluctuations may lead to death from starvation, the likelihood of which increases with the strength and duration of the fluctuations.

Generalization of model of competing benthic herbivores

We completed some theoretical work that generalized previous results of Wilson *et al.* (1999). We now have formalism to describe a situation where two consumers compete for a single resource, but differ in their ability to access and deplete the resource. The two species are referred to as diggers and grazers, where diggers can deplete their resource to lower densities than grazers. Coexistence requires that the grazer species must either move faster than the digger, or convert resources more efficiently.

Model of competing estuarine fish

We have developed a simple model of resource-based competition occurring between two species; one open to immigration and one closed to immigration. Stable coexistence of the two competing species is possible if, and only if, three conditions are satisfied: 1) the species open to immigration is the inferior consumer, i.e. it must not reduce the resource to a level below that usable by the closed species, 2) the loss rate of individuals from the open species exceeds the rate of any gains derived from utilization of the resource, i.e. in the absence of immigration we would expect the population of the open species to decrease to zero, and 3) the immigration rate of new individuals into the population of the open species equals or exceeds this net loss rate, i.e. the open population is maintained solely via the supply of new individuals from outside the population.

To test the predictions, we calculated parameter values from populations of two competing species of fishes commonly found co-occurring in southern California wetlands. Predicted equilibrium biomass densities for the two species were of the same order of magnitude as those observed at our study site, the Carpinteria Salt Marsh, Carpinteria, California (illustrated on next page). Also in accordance with

our predictions, individuals of the closed species, *Gillichthys mirabilis*, were the more efficient consumers of a common prey resource than were members of the open species, *Leptocottus armatus*. Further, overall loss rates of the open species exceeded calculated gains derived from utilization of the resource and this projected deficit was more than compensated for by the immigration rate of new individuals into the open population.

Carpinteria salt marsh, California. The "open" species recruits through the narrow opening to the ocaen. The closed species recruits within the marsh.

Populations of the two species used to test our model never exist at equilibrium densities in the field. Populations of *Leptocottus* in a given estuary consist almost entirely of individuals which entered the system as newly settled juveniles in the spring. These individuals remain in the estuary throughout the summer and then emigrate in the late fall. We investigated the effects of these various population level processes on our model predictions by incorporating the effects of seasonal immigration, emigration, emergence, and local reproduction directly into the model. Adding a seasonal component to our model increased the region of parameter space corresponding to the predicted coexistence of the two species.

Model of Carman's microcosms

We have developed a linear food chain model of experiments by Dr. K. Carman and co-workers (Louisiana State University), who investigated the effects of diesel fuel contamination of a benthic, estuarine, food-web, using microcosms. The key observation in Carman's studies was that increasing levels of diesel are associated with higher densities of microalgae, and a pronounced decrease in density of copepods (the dominant grazers in uncontaminated systems). The model uses three differential equations describing changes in utilizable nitrogen, biomass density of algae, and biomass

(or carbon) density of grazers. Nitrogen becomes available at a fixed rate, and is absorbed by benthic microalgae (BMA), whose growth rate depends on light and available nitrogen. Gazers gain carbon by eating algae and lose carbon through respiration and mortality. With only very general assumptions on functional dependence of rates, we can show that the equilibrium density of BMA is unaffected by an increase in the input flux of nitrogen, but will increase in response to increased loss rates for grazers. This shows that the grazers are certainly implicated in the observed increase in BMA, but does not explain the observed changes in nitrogen flux.

With additional assumptions on functional forms for the physiological rates of algae and grazers, we obtain a model, all of whose parameters can be estimated from literature data, albeit with considerable uncertainty in some cases. This allows us to study transient dynamics over a time period of the same duration as the experiments. Currently, our predicted transients exhibit oscillations which are absent in the data. Resolving the source of this difference between predicted and observed dynamics will help identify critical mechanisms operating in the system.

Ecosystem models

We have started work on a four-level ecosystem model – nuttrients, algae, herbivores, and decomposers, that will be used to model the simultaneous flow of carbon and nitrogen in Carman's microcosms. There are still some unresolved questions relating to the algal and decomposer dynamics.

IMPACT/APPLICATIONS

Our DEB modeling work aims to unify theory describing the effects of environmental stress on diverse range of organisms. A key component is the emphasis on model testing; insight gained here will be applicable in other contexts. The study of competing herbivores takes a very original approach, and opens the possibility of using energetic-based models to relate the outcome of competition to environmental change. The new ecosystem models will link our research to the large body of empirical and theoretical work on the cycling of elemental matter in stressed environments.

TRANSITIONS

The research is not yet at a point to move from research into the Navy fleet or to industry. It has been used in a project related to off-shore oil production.

RELATED PROJECTS

PI Nisbet spent academic year 1998-9 at the National Center for Ecological Analysis and Synthesis (NCEAS) and organized a working group at NCEAS on the theme "Population level effects of toxicants". The working group will bring together for four one-week meetings researchers using different approaches to the problem of relating the effects of toxicants on individuals, populations and ecosystems. Two meetings have been held; two are planned for year 2000. This should lead to improved methodology in future ONR-funded research.

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